Origin and Development of Vessel

Trachea (or vessel) originates from meristematic cells that are grouped together in a longitudinal file. The meristematic cells are known as xylem mother cell that develops from procambial cells in the primary xylem. In secondary xylem cambial derivatives give rise to xylem mother cell. At the last stages of development the fusion of xylem mother cells end to end results in the formation of trachea. Due to fusion and subsequent loss of end walls the vessels are grouped together to form a continuous long tube.

Each xylem mother cell forms a vessel member. The primordial vessel member may or may not elongate in length during differentiation. But it usually widens laterally. Secondary wall materials deposit after the completion of longitudinal elongation and lateral expansion. The deposition does not occur uniformly and forms specific pattern characteristic for the particular vessel element. The secondary wall materials do not cover certain portions of the primary wall.

These portions are the site of future pits and perforations. The cell wall at the future perforation region becomes thicker than the rest of primary walls. The thickening occurs due to the swelling of intercellular pectic substances and no secondary wall material is deposited on it. The swollen regions of primary wall later disintegrate to form perforations. This happens after the completion of deposition of secondary wall substances.

In longitudinal section the end walls of primordial vessel element appear as lens-shaped (e.g. Celery) or plate like (e.g. Robinia) after swelling. As many as three layers can be distinguished in this region. Middle lamella and the two primary walls of the two adjacent cells compose the three layers. The middle lamella consists of pectic substances whereas non-cellulosic polysaccharides compose the two adjacent, primary walls.

Xylem mother cells are thin walled, densely cytoplasmic, uninucleate and vacuolated. Cytoplasm remains active throughout the development of vessel elements. It slowly disintegrates as the vessel members mature. As development progresses the nucleus becomes small and flattened, and lie either at the centre, on the side of lateral wall or against the end wall —the site of future perforation. Differentiating metaxylem becomes polyploid and contains more DNA than neighbouring cells.

In some members of Euphorbiaceae the developing vessel members become multinucleate. Commonly the cells remain uninucleate with large endopolyploid nuclei. At maturity nucleus disintegrates. The tonoplast- bound vacuolar sap contains hydrolytic enzymes. After the rupture of tonoplast cytoplasm and nucleus are exposed to hydrolytic enzymes. As a result autolysis of cytoplasm occurs.

After the introduction of electron microscope it is observed that xylem mother cell contains microtubules, endoplasmic reticulum, dictyosomes and mitochondria etc. Evidences suggest that microtubules direct the deposition of new secondary wall materials. It is observed that the concentration of microtubules increases at the region of developing thickening of wall. Cytoplasm present between the thickenings is devoid of microtubules.

In this region endoplasmic reticulum is present in close association with the plasmamembrane. In the cytoplasm active dictyosomes are also present. It is thought that vesicles produced from dictyosomes

contribute wall components at the site of wall thickenings. The role of endoplasmic reticulum is to inhibit the process of wall thickenings. As the wall reaches its final state of maturity, the vacuoles present in the differentiating vessel member coalesce.

As a result a single large vacuole is formed. Later vacuolar membrane ruptures and this causes the degeneration of cytoplasmic contents. Sometimes mitochondria persist. The end walls of differentiating vessel members ultimately get dissolved and the remnants are swept away by transpiration stream. Thus the developing vessel members are grouped together and converted to a series of connected tubes.

The region of future perforation is clearly set off at an early stage from the secondary wall. It is the common partition wall between the two contiguous cells that are destined to form vessels. The cell wall at this region is composed of primary wall only. During development it swells along with the middle lamella. It becomes thicker than the neighbouring primary wall. Then it along with the adjacent primary wall and middle lamella gets dissolved to form the simple perforation. In other cases small holes appear at the thickened regions, the walls gradually dissolve and form the characteristic perforation plate.

It occurs presumably by the action of still living protoplasts. Thus cell-to-cell continuity is established and a continuous tube is formed. Now the vessels become functional in conduction. Around the simple perforation the secondary wall appears as a rim. The evolutionary specialization of vessel is discussed within the vessel itself along with other features related to it. These include length, end wall pitting, thickening of cell wall and the outline in transverse section of a vessel while the other features comprise the abundance, groupings and ring porousness of vessels.

a. Length:

Vessels have arisen from no other cells than tracheids that are usually long and narrow spindle shaped. So it is assumed that long vessels are primitive. The advanced forms are short and wide.

As specialization increases the length of fusiform initial that forms vessels also reduces. The length of a vessel may be as short as a few centimetres or as long as several metres. The size is not random. It is to be noted that certain organs have only long vessels and others have only short ones.

b. End wall:

Vessel with long slanted end is considered as primitive as it is present in tracheid like vessels. Evolution proceeded towards the formation of transverse end walls.

c. Perforation plate:

Vessels with scalariform perforation plate with many bars in a very slanted end wall is considered as primitive. This type of perforation is associated to long vessel, which is also considered as primitive. During evolutionary specialization the number of bars reduced.

Accordingly the number of pores also reduced. The final stage in specialization is the loss of all bars and simple perforation is the result at the end walls. Simple perforation with circular rim is more advanced than long oval rim (Fig. 10.5).

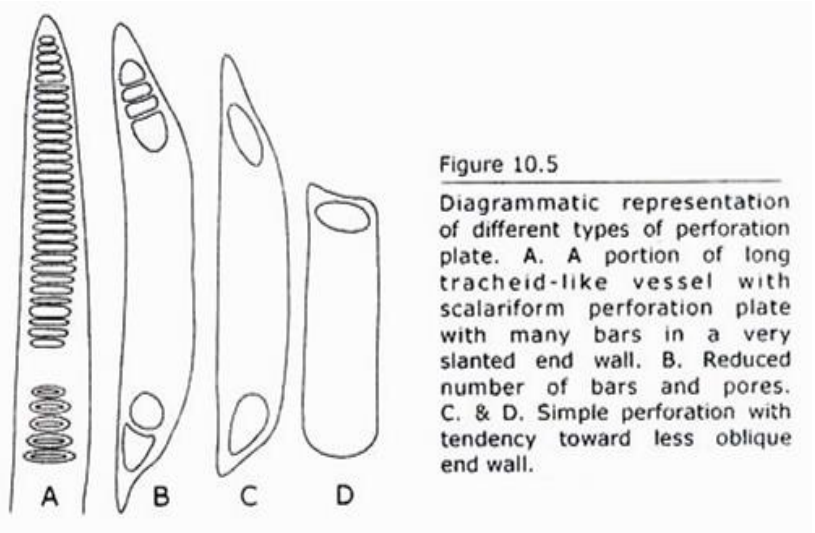

Figure 10.5

Diagrammatic representation of different types of perforation plate. A. A portion of long tracheid-like vessel with scalariform perforation plate with many bars in a very slanted end wall. B. Reduced number of bars and pores. C. & D. Simple perforation with tendency toward less oblique end wall.

The specialized vessels are short with large diameter. The perforation plate is simple with circular rim in an almost transverse end-wall. This type of vessel is advantageous for good conduction of water.

In a wide vessel the adhesive interaction between the molecules of water and cellulose of cell wall is decreased and this minimizes the contact between water and cell wall. As a result water flows easily. Moreover the simple perforation plate with circular rim allows easy flow of water. In scalariform perforation plates the bars may offer resistance to water flow.

The long vessels require extra reinforcement in addition to that provided by the secondary wall. Scalariform bars and the rim of perforation plate provide the extra means of strengthening the long vessel. In short vessels with simple perforation the mechanical strength is obtained from the rim of perforation plates in addition to the secondary wall.

d. Lateral wall pitting:

It is suggested that scalariform pitting is the most primitive. Evolutionary sequence advanced through transitional types to opposite type. The final stage in the evolution is alternate pitting. Scalariform pitting is associated with long vessel, whereas alternate pitting is associated with short vessel. Vessels with medium length are associated with transitional and opposite pitting (Fig. 10.6).

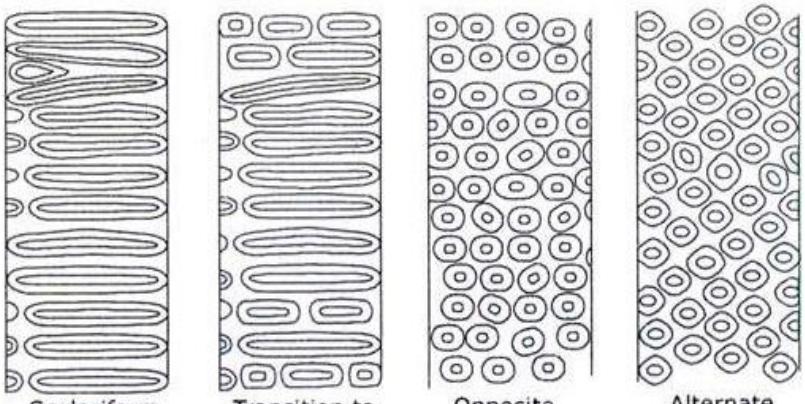

Figure 10.6

Diagram illustrating different types of lateral wall pitting of vessel member.

e. Thickening of cell wall:

Spiral thickening on the secondary wall is an advanced character. This type of thickening is closely linked with ring porousness of wood. Metcalfe and Chalk is of opinion that probably ecological factors associated with ring-porousness are responsible for the correlation.

f. Outline in transverse section:

Vessel, as seen in transverse sections, ranges from angular in outline to circular in outline. It is suggested that transition occurred from angular to circular in outline. This type of transition is observed both in dicots and monocots.

g. Abundance:

The abundance of vessel offers characteristics of taxonomic significance. It is measured as the number of vessels present mm^2 of areas in a transverse section of wood.

h. Grouping:

In the transverse section of wood it is observed that vessels may be present as single or in groups. The groupings may be of multiples of two or three. In a group the vessels may be arranged in radial, oblique, or tangential lines.

This type of distribution and character are considered as most valuable taxonomic character. These characters can be used to trace the trends of evolutionary specialization and to indicate affinity. It is suggested that solitary vessel represents the primitive condition. During specialization vessels are arranged in groups.

i. Ring porousness:

Ring porous wood has two marked zones based upon differential distribution of large and small vessels. In this wood numerous large vessels occur at the beginning of growth ring and fewer small vessels are situated at the end. This type of wood is formed due to either different seasonal climatic variation, cold winters or very dry season followed by wet climate.

In contrast, diffuse porous wood has no marked zones of small and large vessels and their distribution is at random throughout the growth ring. Gilbert (1940), after an extensive study on North Temperate woods opines that ring porosity is an advanced feature. But Carlquist does not consider ring porosity as one of the trend of vessel evolution and showed the occurrence of ring porosity in the South Temperate Zone. Moreover the data obtained by Metcalfe and Chalk are not in correlation with features of vessel advancement. The ring porous feature is present in the vessels of scalariform (primitive) and simple perforation (advanced) with almost equal percentage. Therefore it is concluded that ring porosity represents an ecological specialization of a wood. This is an evolutionary adjustment to seasonal climatic condition. Ring porous wood occurs in widely separated taxonomic groups.

It was previously mentioned that vessels evolved from tracheids. Tracheids are reported from the oldest fossil *Cooksonia* from Upper Silurian deposits. *Cooksonia* is a leafless, rootless vascular plant and consists of a horizontal rhizome and erect stems. The xylem contains annularly thickened tracheids only. *Baragwanathwia*, another early vascular plant, also had tracheids with annular thickenings in the xylem, but in contrast to *Cooksonia* it had leaves.

Vessels are **polyphyletic** in origin. Vessels occur in Pteridophyta (*Selagmella, Equisetum* and the four ferns- *Aetna optens, Pteridium, Marsilea* and *Regnellidium*), Gymnosperm (*Ephedra, Gnetum* and *Welzvitschia*) and angiosperms.

Aside from angiosperms, vessels of the above mentioned genera of Pteridophyta and Gymnosperm are considered as anomalies. Vessels appeared first in the secondary xylem of dicots and later in the primary xylem. In monocots vessels first arose in roots and then later in the stems and leaves.

Origin and Phylogeny of Phloem

1. Sieve Cell-Origin:

The mother cells of sieve cells vary in shape. They are slender, short cylindrical to elongate with both ends tapering. Numerous primary pit fields occur on lateral walls. During differentiation the mother cells elongate. Vacuole appears in the cytoplasm that streams actively. The cell wall increases in thickness. Sieve areas develop in the position of primary pit-fields. Cytoplasmic strands appear in the sieve areas and they gradually become prominent and increase in size. At later stage callose develops surrounding the cytoplasmic strands. Sieve cell predominates in pteridophyte and gymnosperm. It is reported among angiosperms in *Anstrobaileya scandens* and *Sorbus aucuparia* of Rosaceae. Sieve cells are considered as primitive. They are not arranged in axial files. Moreover the structure of end walls is similar to the lateral walls.

2. Sieve Tube:

Sieve tubes are arranged in axial files. The end wall of it is the sieve plate. Sieve plate is a specialized structure and differs from the sieve areas present on the lateral wall of a sieve tube and all walls of a sieve cell.

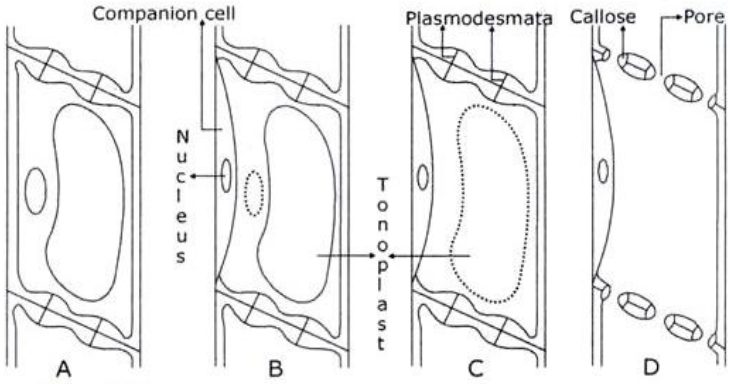

Figure 10.7

Diagram representing the development of sieve tube. A. Sieve tube mother cell that divides longitudinally to form companion cell (B). C. The disappearing tonoplast. D. Mature sieve tube.

i. Origin and development of sieve tube:

Sieve tubes are present in primary and secondary phloem and accordingly they originate from procambium and cambium respectively (Fig. 10.7). The procambium and cambium are arranged in a longitudinal file. They contain living protoplast with prominent nuclei, endoplasmic reticulum, dictyosomes, tonoplast bound vacuoles, ribosomes, mitochondria, chloroplast etc.

The mother cells divide longitudinally to form two daughter cells. One of the daughter cells forms the companion cell and the other cell develops into sieve tube member. During development the companion cell may divide transversely to form more companion cells. The differentiating sieve tube member increases in length and its protoplast undergoes a profound change.

In mature sieve tube mitochondria, plastids, P-protein, plasmalemma and some endoplasmic reticulum persist. The other cellular components degenerate during differentiation. The nucleus disappears or may persist as collapsed body. At early stages of differentiation the endoplasmic reticulum (ER) is of rough type due to the presence of ribosomes. Later ER becomes smooth by loosing the attached ribosomes and aggregation in parallel stacks to form cisternae. The cisternae are arranged in parallel or perpendicular to long axis of the cell wall of the sieve tube member and occupy the parietal position. As development progresses ER diminishes in amount. Some changes also occur in mitochondria where the inner membrane disorganizes and so lacks cristae. The vacuolar membrane ruptures and as a result there lies no delimitation between cytoplasm and vacuole. After the disappearance of tonoplast the P-protein occupies the parietal position of sieve tube member and sieve plate pores.

Sieve areas originate at the sieve plate, which is the common transverse wall of the sieve tube elements. The future sieve plate, at early stages, is smooth with no sign of primary pit fields. Later there appear the plasmodesmata, which mark the site of future sieve area. A single plasmodesma occupies the future pore site. Callose deposits encircling the plasmodesma. Callose accumulates on both sides of the cell wall and assumes the shape of platelets. A pair of callose platelets, which is interrupted at the centre where plasmodesma exists, occupies the future pore site. In between the pair of platelets there occur the primary walls of the two adjacent cells and the middle lamella. Callose deposition continues, platelets increase in thickness, plasmodesmatal canal enlarges and a cavity is developed at the middle lamella region. At a later stage the two cell walls between the paired platelets disappear and thus a pore is formed. The end result is the full differentiation of sieve plate and the protoplast of the contiguous sieve tube elements become continuous.

ii. Phylogeny of sieve tube:

Long sieve tubes are considered as primitive. The short one indicates advanced condition. The cambial initials, during evolutionary specialization, tend to become shortened and this caused the formation of short sieve tubes.

It is frequently noted that cambial initial undergoes transverse septation before the differentiation of sieve tube. As a result short sieve tubes are formed. So, Carlquist opined that the studies on the length of sieve tube must note whether it was directly derived from the cambial initial or formed after the septation of initial.

The sieve tube that has a long end wall with numerous sieve areas is considered as primitive. Small pores in the sieve plate are regarded as primitive by Zahur (1959). Hemenway (1913) regards that the lateral sieve areas, during evolutionary specialization, become smaller and less conspicuous.

The terminal sieve areas become more specialized and form the sieve plate. The sieve plate may be compound or simple and the latter is an advanced feature. The position of a sieve plate also changed

from oblique to almost transverse during phylogenetic advance. So the primitive sieve tube has compound sieve plate with oblique position, whereas the advanced one has simple sieve plate with horizontal orientation. A significant statistical correlation was found between the compound sieve plate and plate with oblique orientation. A similar correlation was also found between simple plate and those that are horizontal in position. Zahur noted that there exists a correlation between the length of a sieve tube and length of a sieve plate. Zahur grouped the sieve tubes into three categories based on the length of it, position of sieve plate and number of sieve areas present per sieve plate. These types were compared to other features in a statistical fashion to indicate phylogenetic advance.

The three categories are:

(1) Sieve tube long, sieve plate is oblique in position and the number of sieve areas is more than ten per plate.

(2) Sieve tube medium in length, sieve plate is oblique in position and the number of sieve areas per plate ranges between two to ten.

(3) Sieve tube is short, sieve plate is almost transverse to transverse in position and the number of sieve area is single per plate.

Zahur concludes that in course of evolution:

(1) The length of sieve tube is decreased and this is due to either reduction in length of cambial initial or septation of the initial;

(2) The length of end walls decreased with the reduction in number of sieve areas per sieve plate;

(3) In the secondary phloem of dicots, the size of sieve areas increased, and

(4) In the functional sieve tube the presence or absence of nucleoli has no phylogenetic significance and this feature may be regarded as taxonomic criteria.

The sequence of specialization in the metaphloem of monocots seems to have occurred in the following way: roots to stems and terminating in rhizomes, corms and inflorescence axes. The least advanced sieve tubes are noted in roots and the most advanced forms are found in rhizomes, corms and inflorescence axes, whereas the intermediate forms are present in the aerial stems.

3. Companion Cell:

The companion cell and sieve tube originate from a common parent cell. It is present in the primary and secondary phloem and accordingly the parent cell originates either from procambium or cambium. The parent cell divides by unequal longitudinal division and the smaller cell develops into companion cell. Companion cells remain associated with sieve tubes. Zahur, in the secondary phloem of dicots, distinguished three types of companion cell to indicate phylogenetic specialization. The basis of distinction is length and septation of companion cell.

The followings are the three types:

(1) Companion cell is much shorter than the accompanying sieve tube.

(2) Companion cell is almost as long as the accompanying sieve tube.

(3) Companion cell is as long as the accompanying sieve tube, but the companion cell is septate. Zahur considers that the above three types form a natural group. Zahur regards that the first type, where the companion cell is much shorter than the accompanying sieve tube, is primitive.

The other two types are advanced. The decrease in the number of companion cell indicates evolutionary advance. In course of evolution the length of sieve tube is shortened. This shortening may be correlated with the increasing contact between the companion cell and sieve tube (Carlquist).

4. Phloem Parenchyma and Fibre:

Procambium gives rise to phloem parenchyma of primary phloem. In secondary phloem the axial phloem parenchyma and phloem rays are developed from fusiform initial and ray initial of cambium respectively. Some parenchyma cells originate from a common mother cell of sieve elements. Fibres occur in both primary and secondary phloem and accordingly their origin differs.

The primary phloem fibre originates from procambium whereas the secondary phloem fibre originates from cambium. The fusiform initial of cambium gives rise to fibre, which composes the axial system of the organ in which it occurs. In many dicotyledonous stems the parenchyma of protophloem often differentiates into fibre in later stages of development, i.e. when the protophloem elements become functionless.

The phloem parenchyma and fibre of secondary phloem bear no phylogenetic trend in phloem evolution. The distribution and morphology of them may be of comparative value (Zahur).

Sieve elements are the most labile cells of a plant. The fossils do not provide any useful details of phloem structure though other tissues show excellent preservation. An idea of fossil phloem can be obtained from *Palmoxylon* and *Rhynia*. Therefore the phylogeny of phloem is inferred from extant plants.